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PRIMARY GEO-ORIENTATION IN SOD WEBWORM MOTHS CLIFFORD S. CRAWFORD

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GRAVITY IS A RELATIVELY UNCHANGING STIMULUS to which animals respond with characteristic primary orientations, these being the positions they adopt when inactive and from which they generally become active. One such response is the common transverse orientation in which "the belly is downward" (Fraenkel and Gunn, 1961). Another primary orientation in animals is manifested by the long axis of the body paralleling the pull of gravity.

Relatively few studies have dealt with the second response. In one of these studies Wilson (1964) carefully recorded many observations of geo-orientation by adults of *Choristoneura fumiferana* Clemens, the spruce budworm. He concluded that most of the time the insect rested in a geonegative (facing upward) position within 30° of the vertical. In another investigation on Lepidoptera Keiper (1968) found that in 14 species of *Catocala* moths adult resting positions were consistently either geopositive or geonegative, depending on the species.

Pyralid moths of the subfamily Crambinae typically inhabit areas where representatives (crops as well as grasses) of the Gramineae abound. Crambinae with grass-feeding larvae are called sod webworm moths and are often encountered resting on grass leaves and stems. The moths are slender, with closely folded wings, and in most instances the angle of inclination of the longitudinal axis parallels the longitudinal axis of the leaf or stem on which the insect is resting. Such positioning renders the resting insect fairly inconspicuous to human observers and presumably to predators as well.

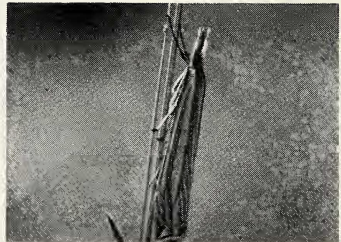
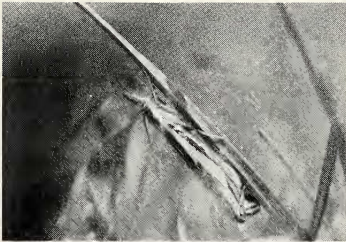
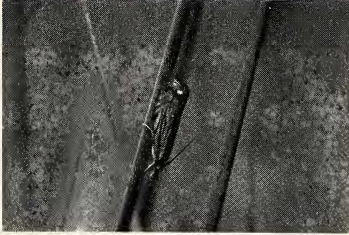


Fig. 1—*Chrysoteuchia topiaria*, male.
 Fig. 3—*Crambus praefectellus*, male.
 Fig. 5—*Crambus whitmerellus*, female.

Fig. 2—*Chrysoteuchia topiaria*, female.
 Fig. 4—*Crambus sargentellus*, male.
 Fig. 6—*Crambus harpipterus*, female.

As will be documented in this paper, some of the resting moths tend to orient geopositively, others geonegatively, and still other species form a third group that is more difficult to characterize in terms of primary orientation to gravity. In addition, secondary geo-orientations, assumed when moths are walking, copulating, and ovipositing, can be superimposed on any of the primary orientations. The object of this paper is to describe the basic primary orientations exhibited by resting sod webworm moths and whenever possible to relate these orientations to groups of taxa. Names of species and genera are based on a continuing revision of the Crambinae by Dr. A. B. Klots (North America) and on the work of the late Dr. S. Bleszynski (elsewhere).

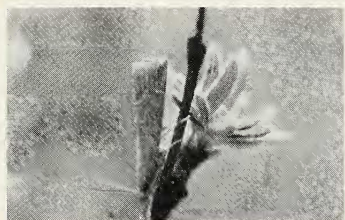
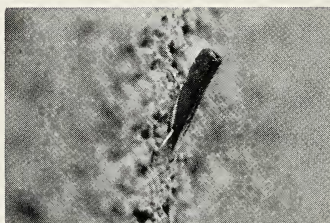
CRAMBINAE WITH TYPICAL GEOPOSITIVE ORIENTATION

Chrysoteuchia topiaria Zeller.—I discuss this insect first, because since it was first reported that the moths “face up or down” (Crawford and Harwood, 1964), it has become apparent from many observations that such an oversimplification must be qualified. The following discussion also illustrates some of the complexities of geo-orientation which probably apply to all species of Crambinae.

Most subsequent observations were made near Portland, Oregon, and at the Middle Rio Grande Experiment Station near Belen, New Mexico, where a population existed for several years on experimental plots of western wheatgrass, *Agropyron smithii* (Crawford, 1967). Other populations were noted in the Brazos, Jemez, and Sangre de Cristo Mountains in northern New Mexico.

Male *C. topiaria* display a strong geopositive tendency upon landing (Fig. 1), an observation confirmed by Klots (personal communication). (As with many crambine adults, the usual landing site is a blade or stem of grass.) When the landing orientation is geonegative the body is usually and rapidly turned 180°. I have frequently followed a single male in flight, noted its orientation on landing, then disturbed it and followed it through additional flights and landings. Seldom has such a male faced away from the ground.

Females usually assume a geopositive orientation, too. In contrast with males, however, they often remain facing upward after landing that way (Fig. 2). In this geonegative position



- Fig. 7—*Crambus teterellus*, male.
 Fig. 9—*Tehama bonifatella*, sex unknown.
 Fig. 11—*Agriphila plumbifimbriella*, female.

- Fig. 8—*Crambus teterellus*, male.
 Fig. 10—*Tehama bonifatella*, sex unknown.
 Fig. 12—*Agriphila plumbifimbriella*, male.

and especially when they are gravid, females of many Crambinae tend to bend the head forward rather than keeping it aligned with the long axis of the body as is the case in positive geo-orientation. At this time the antennae, which are otherwise generally held close to the back, extend approximately at right angles from the body (see Fig. 5 and Fig. 11 for good examples of this posture).

Negative geo-orientation among female *C. topiaria* seems to be most frequent (in daylight hours at least) during the afternoon when oviposition is maximal (Crawford, 1967). Positive geo-orientation does not, however, preclude oviposition. Moths in this position can and do release eggs which occasionally become trapped in the space between the abdomen and the closely folded wings.

Pediasia spp.—Prescott (1965) observed numerous Crambinae in different parts of Oregon. He reports characteristic geopositive orientation during the day for *P. trisecta* Walker and *P. dorsipunctella* Kearfott. I observed large numbers of *P. dorsipunctella* on 14 August, 1964, between Mitchell and Prineville, Oregon. Both sexes were present and settled on grass in a stand of large ponderosa pines. All individuals faced down, with wings and abdomen projecting outward from the grass stalk.

Klots (personal communication) states that *P. mutabilis* (Clemens), which is not closely related to the above species in this very diverse genus, "is the most extreme species I know for resting head down." According to Ainslie (1923a), "They alight abruptly, usually on a grass stem, and instantly turn head downward and stand with the head pressed closely to the stem and the body elevated at a considerable angle."

I have observed *P. luteolella* Clemens males oriented geopositively in the Jemez Mts. One female displayed negative geo-orientation. Prescott (1965) states that the resting posture is "face down."

Others.—According to Hudson (1928) *Crambus tuhualis* Felder from New Zealand holds its wings "upwards at an angle of about 15 degrees from the object on which this insect is standing." Judging from the portrait of this species in Hudson's book I strongly doubt that it really belongs in the newly revised genus *Crambus* (sensu stricto).

CRAMBINAE WITH TYPICAL
GEONEGATIVE ORIENTATION

Crambus spp.—Geonegative resting orientation seems characteristic of both sexes in a number of species in this genus.

Crambus tutillus McDunnough was abundant in grass fields near Portland, Oregon, during June in 1963 and 1964. Mr. Hubert Prescott and I spent a profitable afternoon in the field together exchanging notes on the behavior of this species, and he subsequently reported on the resting posture (Prescott, 1965). I noted that while females when viewed from the side closely resembled the lateral aspect of geonegatively oriented *Chryso-teuchia topiaria*, *C. tutillus* males tended to hold the head in the plane of the body axis and to keep the antennae against the back. This posture appears to hold generally for other male *Crambus*. However, during sexual activity male antennae are often held horizontally and tend to wave, probably in response to pheromones released from females.

Crambus cyrilellus Klots was observed in central New Mexico in July and August. Individuals of both sexes showed a geonegative resting posture.

Crambus praefectellus (Zincken), a widely distributed species in the United States, is fairly common in the Jemez Mts. of New Mexico. Observations of individuals in the field and of laboratory-reared specimens disclosed that geonegative orientation is typical of this group (see Fig. 3) although I have seen some individuals that occasionally oriented themselves otherwise. According to Ainslie (1923b), they seldom "rearrange their position after lighting," and instead of elevating the posterior of the body at a slight angle, maintain the body "closely parallel with the surface on which they rest."

Crambus sargentellus Klots flies in late spring and early summer in the Jemez Mts. Its geonegative resting behavior was seen both in wild individuals (nearly all males) and in females confined to vials during oviposition tests. Figure 4 shows a male at rest.

Crambus whitmerellus Klots was captured infrequently in high meadows in the Jemez and Sangre de Cristo Mountains. Resting behavior in this species (see Fig. 5) is very similar to that of *C. sargentellus*.

Crambus harpipterus Dyar is another Jemez Mts. crambine, both sexes of which invariably face upward when settled. I have had ample opportunity to observe the behavior of these

moths in July and August from 1966 to 1969. Figure 6 shows a female at rest.

Crambus cypridalis Hulst is a late-summer flier in the Pacific Northwest, where Prescott (1965) reported that its resting position was geonegative.

Crambus biothanatalis Hulst, according to Prescott (1965) in Oregon, has a resting posture of "head up." An additional comment on this species is given at the end of this paper.

Argyria spp.—Klots (personal communication) states that those he has seen [*A. nivalis* (Drury), *A. auratella* (Clemens), and *A. critica* (Forbes)] "rest head up." He considers that these are not *Argyria* in the strict sense.

CRAMBINAE WITH TYPICAL MIXED GEO-ORIENTATION

Crambus teterrellus (Zincken).—Not a *Crambus* in the strict sense (Klots, personal communication), this species on first examination exhibits a simple enough pattern of mixed geo-orientation, sometimes resting geopositively, sometimes geonegatively, and sometimes somewhere in between. When subjected to further scrutiny, however, the pattern is found to be qualified by physical, temporal, and perhaps sexual attributes. Ainslie (1930) reported that these moths rest on grass only infrequently during the day. Instead they prefer as resting sites broad-leaved plants (see Fig. 7), walls of buildings, and other objects. During the warmest and brightest time of day they are quiescent. When resting on leaves they assume a variety of positions. On walls, however, they frequently face downward (Fig. 8). In doing so they closely resemble *Pediasia* species. During the early afternoon in late August I once noted that out of the first 100 individuals counted on a single large wall, 98 were oriented in a distinctly geopositive manner. Yet at night, when both sexes are active, females especially and males frequently land upright on grass and other objects.

Tehama bonifatella (Hulst).—In the two regions where I observed this species, I was unable to characterize its geo-orientation as anything but mixed. This consideration is true for the few specimens seen in the Jemez Mts. of New Mexico (see Fig. 9-10) and for the many viewed near Portland, Oregon. During the day I once released about 20 specimens into a room. Most landed on walls, and their long axes presented no consistent geo-orientation pattern. Prescott (1965) considers their resting posture to be "head up or indifferent."

Agriphila spp.—The resting geo-orientation of at least three species in this genus has been recorded. Burton (1968) noted that in England *A. tristella* (Denis and Schiffermüller) “spend the day sitting head downwards on grass-stems.” Prescott (1965) remarks that in Oregon the resting posture of *A. vulgivagella* Clemens is “probably head down.” My extensive observations of *A. plumbifimbriella* Dyar in New Mexico suggest to me that both the above authors were recording primarily the geo-orientations of males. Certainly males of *A. plumbifimbriella* are much more conspicuous than are females during the daytime. Females stay in grass close to the ground and seldom fly in daylight. When disturbed, they occasionally fly, but also tend to drop to the ground and appear dead. Females seem to rest geo-negatively much of the time, especially when ovipositing during the afternoon (Fig. 11). Males, however, very often face downward during the day (Fig. 12). Yet this diurnal orientation by males is by no means invariable.

Euchromius sp., probably *ocelleus texanus* (Robinson).—Observations in different parts of New Mexico lead me to conclude that this insect rests geo-negatively more often than not. Geo-positive orientation seems to occur about one-fourth of the time.

DISCUSSION AND CONCLUSIONS

Although the observations reported above are limited to relatively few species in the large subfamily Crambinae, certain group-related patterns of geo-orientation are evident. The consistency of the patterns is probably greatest when one considers only resting males, especially in species not exhibiting mixed geo-orientation.

Without exception, at least to my knowledge, observations of resting individuals in the genus *Crambus* (s.s.) have shown their primary geo-orientation typically to be negative. Only eight species of *Crambus* are discussed in this paper; however, I feel that eight is a sufficient number to allow a prediction that negative geo-orientation obtains for the other members of this genus. If the prediction is valid, then we have an instance of a stereotyped behavior pattern that augments a taxonomic grouping based on morphology.

While negative geo-orientation has so far been restricted to species of *Crambus*, and to several species once listed under *Argyria*, the opposite resting posture is also characteristic of at least one newly established genus. Membership in *Pediasia* may

well be associated with positive geo-orientation by resting moths. Geo-orientation in *Chrysoteuchia* other than *C. topiaria* has apparently not been reported. The genus seems well represented in the Palearctic (Bleszynski, 1965). Perhaps this study will stimulate European lepidopterists to make appropriate observations.

Mixed geo-orientations, as I have referred to them, are definitely found in one—and most likely in three species of *Agriphila*. According to Klots (personal communication) the species called *Crambus biothanatalis* by Prescott (1965) is really an *Agriphila*. Prescott's notation of its geonegative orientation (see above) suggests that more and careful recordings of *Agriphila* resting positions be made to determine if mixed geo-orientation is indeed a trait of this genus. My observations on *Crambus teterrellus*, *Tehama bonifatella*, and *Euchromius ocellus texanus* suggest to me that mixed geo-orientation will be found in many other crambine species.

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